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THE INTERRELATIONSHIPS OF PELYCOSAURS

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ABSTRACT. An analysis of 17 characters forms the basis of a hypothesis of relationships of seven pelycosaur genera. These genera include representatives from most of the higher taxa recognized by Romer and Price (1940). In agreement with the phylogeny proposed by Romer and Price, *Edaphosaurus* is considered to be more closely related to *Dimetrodon* than is *Ophiacodon*. In contrast to the phylogeny proposed by Romer and Price, *Ophiacodon* is considered more closely related to *Dimetrodon* than are *Varanops* and *Aerosaurus*. Three character-states that are interpreted as being derived are shared by *Casea*, *Varanops*, and *Aerosaurus*, suggesting that these three genera are members of a clade distinct from the clade including *Ophiacodon*, *Edaphosaurus*, and *Dimetrodon*.

INTRODUCTION

Pelycosaurs occupy a central position in amniote evolution. As a paraphyletic taxon within the clade including mammals, pelycosaurs have played an important role in considerations of the origin of mammals. Also, pelycosaurs include some of the most primitive known reptiles, and are an important element in consideration of the early evolution of amniotes. Thus, an understanding of pelycosaur interrelationships has implications for many broader problems of reptile diversification.

Pelycosaurs were the subject of a detailed monographic study by Romer and Price (1940), and as a result are one of the best understood groups of Paleozoic reptiles. Romer and Price used evolutionary systematics in their study of pelycosaurs (Fig. 1A). In line

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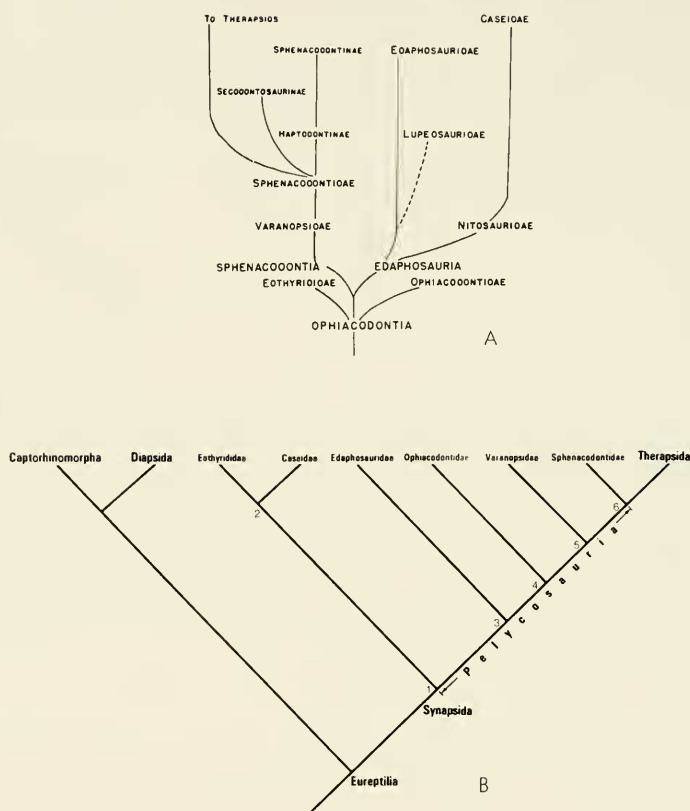


Figure 1. Hypotheses of pelycosaur interrelationships. A) Phylogeny of pelycosaurs presented by Romer and Price (1940); B) Cladogram showing the interrelationships of pelycosaurian families presented by Reisz (1980). A is from Romer and Price, 1940; B is from Reisz, 1980.

with this approach, taxa were established on the basis of phenetic similarity. This is reflected in the diagnoses, which consist of generalized descriptions that encompass the anatomy of most of the members of the group. The taxonomic rank assigned to a group was based on both the diversity within the assemblage and the morphological distance between that and other groups. Ecological interpretations also played a significant role in their study of pelycosaur evolution, and a scenario uniting the morphological and ecological interpretations was developed.

Some aspects of the phylogeny proposed by Romer and Price were brought into question by Langston (1965), who proposed a close relationship between *Oedaleops* and *Eothyris*, and argued that these genera were close to the ancestry of caseids. This implied that caseids were not closely related to the edaphosaurids, as was suggested by Romer and Price.

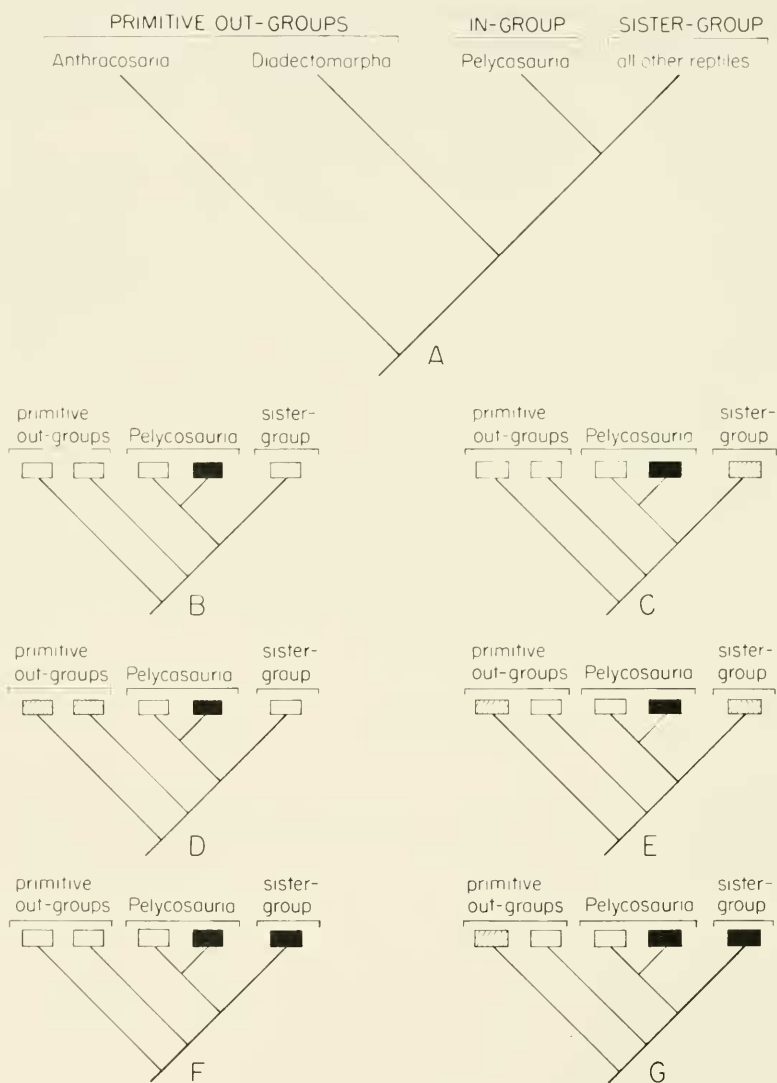
Recently, Reisz (1980) reviewed pelycosaur interrelationships using a cladistic analysis of the characters available to Romer and Price. Reisz concluded that many of the families recognized by Romer and Price were monophyletic, but the interrelationships of the families that Reisz proposed (Fig. 1B) differed from those suggested by Romer and Price. Also, the relationships that Reisz recognized did not conform to the scenario of pelycosaur evolution proposed by Romer and Price.

During the study of a new pelycosaur from El Cobre Canyon, New Mexico, it became clear that much additional morphological information could be brought to bear on the problem of pelycosaur interrelationships, and a review of the group was undertaken. The results of this review are intended to provide a testable hypothesis of pelycosaur interrelationships, and to serve as a framework in which detailed taxonomic and morphological revisions of individual genera and families can be interpreted.

MATERIALS AND METHODS

The central problem in a cladistic analysis is establishing the polarity of character-states. Out-group comparison has been considered the most powerful tool for this (Watrous and Wheeler, 1981). The interrelationships of the groups used in determining the polarity of character-states within pelycosaurs are shown in Figure 2A. These relationships are based on Carroll (1970), except for the position of *Diadectes*, which, following Heaton (1980), is placed with *Limnoscelis* and *Tseajaia* in the Diadectomorpha. Also, following Kemp (1980), pelycosaurs are considered to be the sister-group of all other reptiles.

In using out-group comparison to interpret polarities, two principles are used. One is the principle of parsimony: the hypothesis of polarities that requires the least number of evolutionary events to account for the distribution of character-states will be accepted.



This principle is the basis for the interpretation of polarities for the character-states whose distribution is shown in Figure 2B-E.

The second principle is the co-occurrence of primitive character-states. According to this principle, primitive character-states tend to occur together. Using this principle, the character-state that occurs in the outgroup that, on the basis of other evidence, is thought to be more primitive is accepted as the primitive character-state. This is the basis for the interpretation of polarities for the character-states whose distribution is shown in Figure 2F and G. It should be noted that implicit in this principle is the assumption that reversals are less likely to occur than are independent acquisitions. The use of this principle, therefore, limits the extent to which the results presented here can be used to test this assumption.

Characters of uncertain polarity will not be used to support relationships. However, such characters may provide corroboration of relationships proposed on the basis of derived character-states, since the distribution of uncertain character-states will be either consistent with the cladogram or will require that the occurrence of parallel evolution be hypothesized.

One of the problems in the study of the evolution of groups represented by fossil material is the incorporation of data both from well-known animals and from animals represented by incomplete specimens. This is especially true in the study of the evolution of early reptiles, where material is rare and, in many cases, animals are represented by single fragmentary specimens. Often animals represented by such material have been assigned to a taxon erected on the basis of well-known animals, and discussions of the evolution of the group have focused on the interrelationships of the higher taxa.

Figure 2. The interpretation of polarities of character-states by outgroup comparison. A) Cladogram showing the interrelationships of the taxa used as out-groups for interpreting the polarity of character-states within pelycosaurs; *Diadectomorpha* includes *Diadectes*, *Limnoscelis*, and *Tseijiaia*. B-G) Interpretation of polarities of character-states. In B-E, this is based on parsimony, in F and G, this is based on the principle of co-occurrence of primitive character-states. ■ represent the derived in-group character-states; □ represent the primitive in-group character-states; ▨ represent character-states not present in the in-group.

In order that information from both fragmentary and well-known animals can be incorporated into the analysis of pelycosaur interrelationships, this study will be separated into two steps. The first will be to construct a cladogram showing the interrelationships of the most completely known genera using all available morphological features. This will provide a framework in which data from the less well known genera can be interpreted. The results of this part of the study are presented here. The second part will be the inclusion of the less well known animals in the analysis. Through this, the cladogram will be tested and a more detailed understanding of pelycosaur interrelationships will be obtained.

By using genera as the basis for considering pelycosaur interrelationships, all morphological diversity known to be present within higher taxa will be incorporated in a single analysis of diversification of pelycosaur. Also, assumptions about pelycosaur evolution are minimized. Some currently recognized higher taxa are almost certainly monophyletic and could be treated as units in a discussion of pelycosaur interrelationships. Others, such as the Ophiacodontidae, as currently defined may be either polyphyletic or paraphyletic. By treating each genus as an independent entity, this potential source of error is avoided.

The pelycosaurs considered here are *Casea*, *Varanops*, *Aerosaurus*, *Ophiacodon*, *Edaphosaurus*, *Dimetrodon*, and *Sphenacodon*. The restriction of the study to these genera was necessitated by the accessibility of material for direct observation and the fragmentary nature of available specimens of other genera. Only characters that were actually observed were utilized in the analysis, and many of the reconstructions presented here are modified from previously published reconstructions on the basis of observations made during the course of this work. This required that a large amount of material be examined, and supplying a complete list of specimens studied is not possible. To facilitate future work, the specimens that showed particular structures most clearly are listed in Table 1, and the specimens that are the basis for the modifications in the reconstructions are listed in the figure legends. In all the features considered here, *Sphenacodon* and *Dimetrodon* are indistinguishable (Eberth, 1981). Thus, illustrations from only one of these genera are included here.

Table 1. List of specimens preserving the structures described in the text.

Character	<i>Casea</i>	<i>Varanops</i>	<i>Ophia-</i> <i>codon</i>	<i>Edapho-</i> <i>saurus</i>	<i>Dime-</i> <i>trodon</i>
Supraoccipital	UC 698	—	MCZ 1366	MCZ 1762	MCZ 1347
Tabular	UC 698	—	MCZ 1426	MCZ 1762	MCZ 1347
Basipterygoid tubercula	UR 1011	—	MCZ 4920	MCZ 1531	MCZ 1697
Stapes	UC 698	P 12841	MCZ 1350	MCZ 1762	MCZ 1347
Quadrate ramus of pterygoid	UC 698	P 12841	MCZ 1350	MCZ 1762	MCZ 5950
Basisphenoid shelf	UC 698	UR 2423	MCZ 4820	MCZ 1531	MCZ 1697
Frontal	UC 656	UR 2423	MCZ 1366	MCZ 4309	MCZ 4430
Maxilla	UC 698	UR 2423	MCZ 1366	MCZ 1762	MCZ 1347
Premaxilla	UC 698	MCZ 1926	MCZ 1366	MCZ 1680	MCZ 4982
Quadratojugal	UC 656	UR 2423	MCZ 1366	MCZ 1762	MCZ 6173
Pterygoideus process	—	MCZ 1926	MCZ 1203	MCZ 1370	MCZ 3244
Angular	UC 698	UR 2423	MCZ 1203	MCZ 1370	MCZ 7539
Vertebrae	UC 883	MCZ 1926	MCZ 5912	MCZ 1754	MCZ 5210
Humerus	UC 656	UR 695	MCZ 1486	MCZ 3417	MCZ 8708
Postparietal	UC 698	—	—	MCZ 1762	MCZ 1347
Paroccipital process	UC 656	UR 2423	MCZ 1426	MCZ 1762	MCZ 1347

Abbreviations: UC, UR, and P: specimens housed in the Field Museum of Natural History; MCZ: specimens housed in the Museum of Comparative Zoology.

CHARACTER ANALYSIS: 1. FEATURES FOR WHICH POLARITY CAN BE INTERPRETED

Ventral Margin of Skull

In *Dimetrodon*, *Sphenacodon* (Fig. 3F), *Edaphosaurus* (Fig. 3E), and *Ophiacodon* (Fig. 3D), the ventral margin of the cheek region of the skull is concave (i.e., bowed upward).

In *Casea* (Fig. 3B), *Varanops* (Fig. 3C), and *Aerosaurus* (Langston and Reisz, 1981), the ventral margin is convex and extends below the level of the tooth row.

The ventral margin of the cheek is convex in *Limnoscelis* (Romer, 1946), *Diadectes* (Fig. 3A), and anthracosaurs (Panchen, 1970). In *Hylonomus*, the cheek margin is straight (Carroll, 1964). Thus, three character-states can be recognized: the presence of a concave ventral cheek margin, a convex ventral cheek margin, and a straight

ventral cheek margin. They have the distribution shown in Figure 2C, with the derived character-state present in pelycosaurs being the presence of a concave cheek margin. The condition seen in *Hylo-nomus* is a separate, derived character-state.

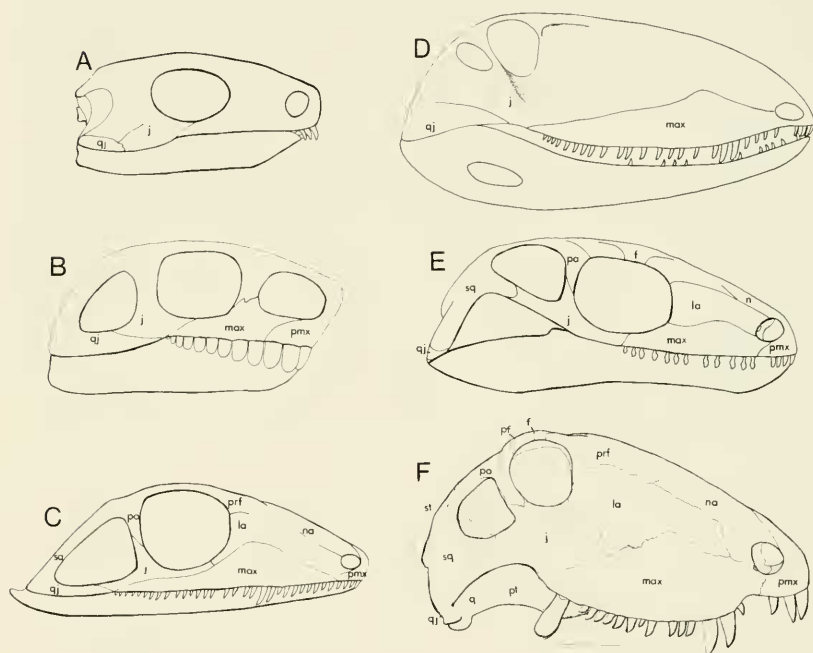


Figure 3. The skulls in right lateral view of A) *Diadectes*; B) *Casea*; C) *Varanops*; D) *Ophiacodon*; E) *Edaphosaurus*; and F) *Sphenacodon*. Drawing of *Diadectes* based on MCZ 1739, MCZ 1736, and MCZ 2086; *Casea* based on UC 698 and UC 656; *Varanops* based on MCZ 1926 and UR 2423; *Ophiacodon* based on UC 671; *Edaphosaurus* based on MCZ 1762, MCZ 1764, and USNM 299844; *Sphenacodon* from Eberth (1981).

Abbreviations: f, frontal; j, jugal; la, lacrymal; max, maxilla; na, nasal; pf, post-frontal; pmx, premaxilla; po, postorbital; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sq, squamosal; st, supratemporal.

Premaxilla

In *Dimetrodon*, *Sphenacodon* (Fig. 3F), *Edaphosaurus* (Fig. 3E), and *Ophiacodon* (Fig. 3D), the anterior margin of the premaxilla slopes posteriorly from the anterior termination of the tooth row giving a convex outline to the snout.

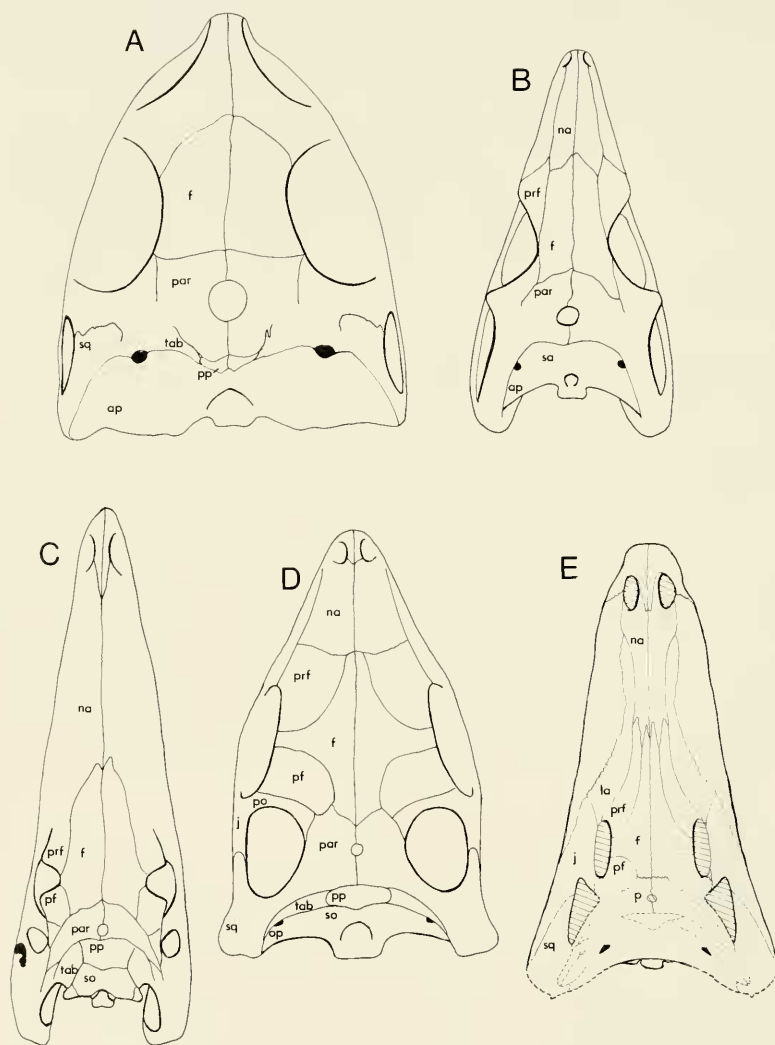
In *Casea* and *Varanops* (Fig. 3B–C), the anterior margin of the premaxilla first extends anteriorly from the anterior termination of the tooth row, giving a forwardly projecting rostrum. Langston and Reisz (1981) argue that the forward sloping premaxilla seen in *Aerosaurus* specimen UCMP 40096 is a result of displacement of the element, and they reconstruct the skull with a posteriorly sloping premaxilla. However, apart from the slope of the premaxilla, there is no direct evidence that the premaxilla has been displaced, and no evidence that the structure of this part of the skull was different than in *Varanops*.

In *Diadectes*, the dorsal process of the premaxilla is vertical (Fig. 3A). *Limnoscelis* is like *Varanops*, *Casea*, and *Aerosaurus* in having a forwardly projecting rostrum (Romer, 1946). Anthracosaurs, with an elongate, flattened face, are not directly comparable to either condition seen in pelycosaurs. The structure of the premaxilla in *Hylonomus* and *Paleothyris* is not known for certain. In *Romeria*, the dorsal ramus of the premaxilla is nearly vertical (Heaton, 1979), a condition not specifically similar to either of the character-states present in pelycosaurs. Thus, these character-states have the distribution shown in Figure 2E, with the presence of a forwardly sloping dorsal ramus of the premaxilla being the primitive condition.

Frontals

In *Dimetrodon* and *Sphenacodon* (Fig. 4E), the frontal has a laterally directed lappet that is greater in mediolateral width than is the posterior end of the frontal. *Edaphosaurus* was figured as having a broad flange extending laterally along the entire anterior half of the frontal by Romer and Price (1940). However, isolated frontals show that the lateral flange illustrated by Romer and Price is formed in part by the prefrontal, and that a lateral lappet like that of *Dimetrodon* and *Sphenacodon* is present (Fig. 4D).

In *Ophiacodon* (Fig. 4C), the frontal is without a strongly developed lateral lappet. A small projection extends between the base of



the prefrontal and postfrontal, but the width of this is much less than the width of the posterior end of the frontal.

In *Casea* (Fig. 4A), *Varanops* (Fig. 4B), and *Aerosaurus* (Langston and Reisz, 1981), frontal lappets are absent.

Frontal lappets are absent in *Limnoscelis* (Romer, 1946), *Diadectes* (Lewis and Vaughn, 1965), anthracosaurs (Panchen, 1970), and *Paleothyris* (Carroll, 1969). Thus, these character-states have the distribution shown in Figure 2B, with the absence of a frontal lappet being the primitive character-state.

Maxilla

In *Dimetrodon*, *Sphenacodon* (Fig. 3F), *Edaphosaurus* (Fig. 3E), and *Ophiacodon* (Fig. 3D), the maxilla does not extend posterior to the orbit and does not meet the quadratojugal. In *Varanops* (Fig. 3C) and *Aerosaurus* (Langston and Reisz, 1981), the maxilla extends posterior to the orbit and meets the quadratojugal, excluding the jugal from the ventral margin of the skull. In cross section, the jugal slopes laterally so that a ridge is present at the contact of the jugal and maxilla. In *Casea* the maxilla meets the quadratojugal, excluding the jugal from the ventral margin of the skull (Fig. 3B). A ridge is present along the contact of the maxilla and jugal as in *Aerosaurus* and *Varanops*.

Thus two structural patterns are present: the *Dimetrodon* pattern in which the jugal enters the ventral margin of the skull and no ridge is present at the contact of the jugal and maxilla, and the *Varanops* pattern in which the jugal is excluded from the ventral margin of the skull by a contact between the maxilla and quadratojugal and a ridge is present along the contact of the maxilla and jugal. *Diadectes* (Fig. 3A), *Limnoscelis* (Romer, 1946), *Paleothyris* (Carroll, 1969),

Figure 4. The skulls in dorsal view of A) *Casea*; B) *Varanops*; C) *Ophiacodon*; D) *Edaphosaurus*; and E) *Sphenacodon*. Reconstruction of *Casea* based on UC 656 and UC 698; *Varanops* based on MCZ 1926 and UR 2423; *Ophiacodon* based on MCZ 1366; *Edaphosaurus* based on MCZ 1762 and USNM 299844; and *Sphenacodon* from Eberth (1981).

Abbreviations: f, frontal; j, jugal; la, lacrymal; na, nasal; op, opisthotic; p, parietal; pf, postfrontal; prf, prefrontal; so, supraoccipital; sq, squamosal; tab, tabular.

and anthracosaurs (Panchen, 1970) are like *Dimetrodon* in these features. Thus, these character-states have the distribution shown in Figure 2B, with the absence of a contact between the maxilla and quadratojugal and the absence of a ridge along the contact of the maxilla and jugal being the primitive character-state.

Quadratojugal

In *Dimetrodon* and *Sphenacodon* (Fig. 3F), the quadratojugal is a small bone sitting on the posterolateral corner of the quadrate and is without an anterior zygomatic process.

Edaphosaurus was reconstructed with a large quadratojugal (Romer and Price, 1940), but specimen MCZ 1762 shows that a small quadratojugal like that of *Dimetrodon* was present (Fig. 3E).

In *Ophiacodon* (Fig. 3D), *Varanops* (Fig. 3C), *Aerosaurus* (Langston and Reisz, 1981), and *Casea* (Fig. 3B), the quadratojugal extends forward from the posterior corner of the skull forming the ventral border of at least the posterior half of the cheek.

In *Diadectes* (Fig. 3A), *Limnoscelis* (Romer, 1946), anthracosaurs (Panchen, 1970), and *Paleothyris* (Carroll, 1969), the quadratojugal is a large element extending well anteriorly. Thus, these character-states have the distribution shown in Figure 2B, with the presence of a large quadratojugal being the primitive condition.

Quadrate Ramus of Pterygoid

In *Dimetrodon* (Fig. 5F), *Sphenacodon*, and *Edaphosaurus* (Fig. 5E), the quadrate ramus of the pterygoid is a vertical sheet with a rounded ventral edge. In *Ophiacodon* (Fig. 5D), *Varanops* (Fig. 5C), and *Casea* (Fig. 5B), a shelf extends medially from the ventral edge of the quadrate ramus, flooring the lateral most part of the tympanic cavity. The quadrate ramus of the pterygoid in *Diadectes* has a similar shelf (Fig. 5A), as does *Limnoscelis* (Romer, 1946). In anthracosaurs, a tympanic shelf is not present, but the quadrate ramus of the pterygoid is little differentiated from the more anterior part of the bone (Panchen, 1970), and is not comparable to the quadrate flange of pelycosaurs in structural details. *Paleothyris* is like *Dimetrodon* and *Edaphosaurus* in not having a medially directed tympanic flange. Thus, these character-states have the distribution shown in Figure 2G, with the presence of a medially

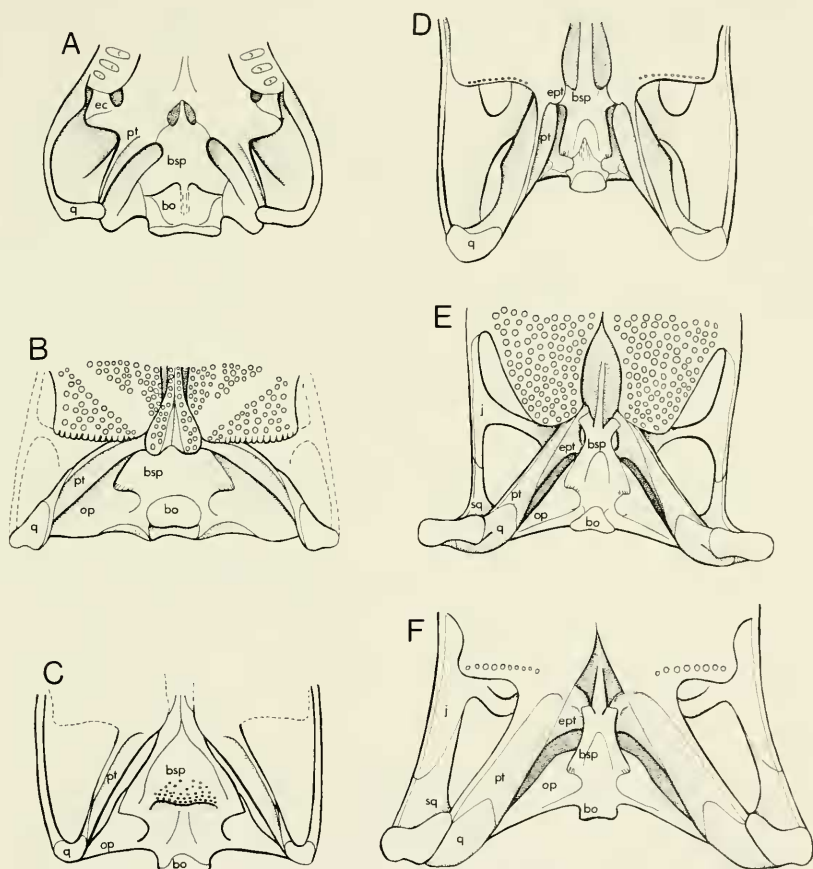


Figure 5. Ventral view of the posterior half of the skulls of A) *Diadectes*; B) *Casea*; C) *Varanops*; D) *Ophiacodon*; E) *Edaphosaurus*; F) *Dimetrodon*. Reconstruction of *Diadectes* based on MCZ 1739 and MCZ 2042; *Casea* based on UC 698; *Varanops* based on P 12841; *Ophiacodon* based on MCZ 1366 and UC 1638; *Edaphosaurus* based on MCZ 1762; and *Dimetrodon* based on MCZ 1365, MCZ 2168, and MCZ 5950.

Abbreviations: bo, basioccipital; bsp, pasisphenoid; ec, ectopterygoid; ept, epipterygoid; j, jugal; op, opisthotic; pt, pterygoid; q, quadrate; sq, squamosal.

directed shelf flooring the tympanic cavity being the primitive character-state and the absence of this flange being a derived condition.

Supraoccipital

In *Dimetrodon*, *Sphenacodon* (Fig. 6D), *Edaphosaurus* (Fig. 6C), and *Aerosaurus* (Langston and Reisz, 1981), the supraoccipital has an area dorsal to the posttemporal fenestra forming the dorsal margin of the posttemporal fenestra, termed the lateral process by Romer and Price (1940). In *Ophiacodon* (Fig. 6B), the supraoccipital is without an ossified lateral process. Romer and Price interpreted the absence of a lateral process as a result of the tendency for poor ossification in that genus, and reconstructed cartilaginous lateral processes. Reisz (1980) accepted this hypothesis and showed a lateral process of the supraoccipital bordering the posttemporal fenestra in his reconstruction of the occiput of *Ophiacodon*. While cartilaginous lateral processes of the supraoccipital may have been present, these would not have been visible in posterior view since the tabular of *Ophiacodon*, as illustrated by Romer and Price (1940), contacts the opisthotic and has a finished ventral surface that would have formed the dorsal edge of the posttemporal fenestra. In *Casea* (Fig. 6A), the arrangement of the supraoccipital and tabular is like that of *Ophiacodon*: the supraoccipital is not exposed above the posttemporal fenestra when seen in occipital view, and the tabular contacts the paroccipital process, excluding the supraoccipital from the margin of the posttemporal fenestra.

In *Diadectes*, the elements of the occiput are fused. In *Limnoscelis*, the relationships of the tabular are like those of the *Ophiacodon* (Romer, 1946). *Paleothyris* is without lateral processes on the supraoccipital, and the dorsal margin of the posttemporal fenestra is formed by the tabular (Carroll, 1969), as in *Ophiacodon*. However, in contrast to that genus, *Paleothyris* has a large posttemporal fenestra that is bounded medially by the supraoccipital, and thus is not distinctly like either condition seen in pelycosaurs. Thus, these character-states have the distribution shown in Figure 2E, with the exclusion of the supraoccipital from the border of the posttemporal fenestra by the tabular being the primitive character-state, and the presence of a lateral process of the supraoccipital forming the dorsal border of the posttemporal fenestra being a derived character-state.

Basipterygoid Processes

The basipterygoid processes of *Dinnetrodon* (Fig. 7G), *Sphenacodon*, and *Edaphosaurus* (Fig. 7F) extend anteriorly, ventrally, and laterally from the lateral surface of the basisphenoid. Each articular surface is divided into two areas, a flat anteroventrally facing area and a dorsally facing area at nearly 90 degrees to this.

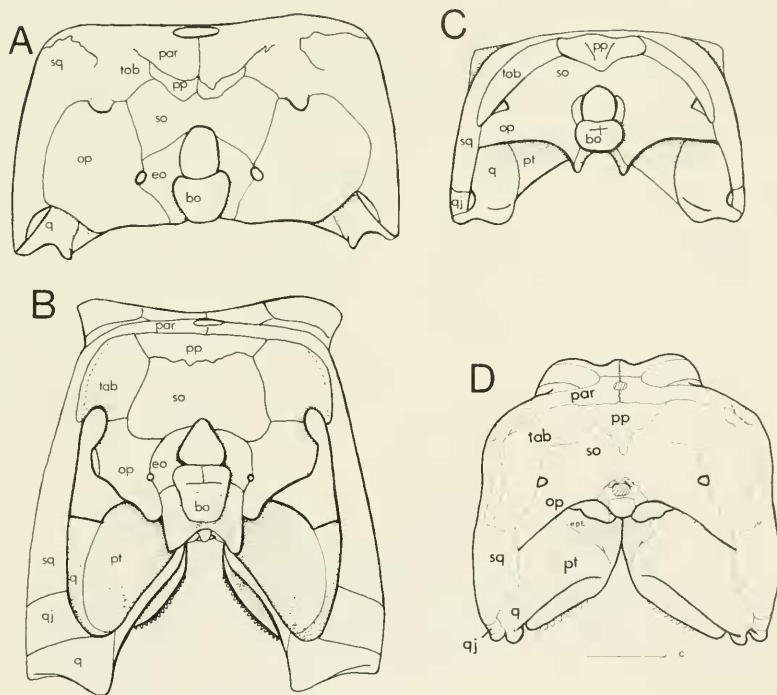


Figure 6. Occipital view of the skulls of A) *Casea*; B) *Ophiacodon*; C) *Edaphosaurus*; and D) *Sphenacodon*. Drawing of *Casea* based on UC 698 and UC 656; *Ophiacodon* based on MCZ 1366, MCZ 1426, and MCZ 1121; *Edaphosaurus* based on MCZ 1762; and *Sphenacodon* from Eberth (1981).

Abbreviations: bo, basioccipital; eo, exoccipital; op, opisthotic; par, parietal; pp, postparietal; q, quadrate; qj, quadratojugal; sq, squamosal; tab, tabular.

In *Ophiacodon*, the basiptyergoid processes extend ventrally (Fig. 7E). The long axis of the articular surfaces are anteroposteriorly oriented and the surface curves smoothly from its ventral to its lateral aspect.

In *Casea* (Fig. 7C), the basiptyergoid processes extend laterally from the side of the cultriform process and have strongly curved articular surfaces. *Aerosaurus* (Langston and Reisz, 1981) is similar to *Casea*, but differs in that the articular surfaces are more elongate mediolaterally.

Thus, two distinct characters can be recognized in the structure of the basiptyergoid process. One of these is the curvature of the articular surfaces: the curved articular surfaces such as are seen in *Aerosaurus* being one character-state and two flat articular surfaces set at

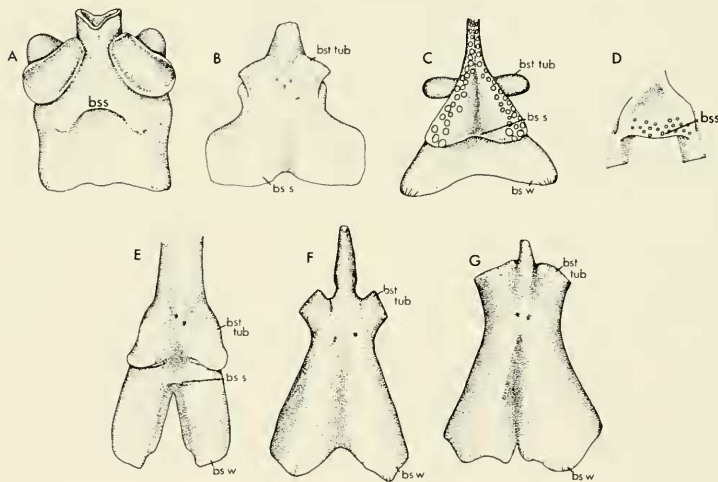


Figure 7. The basisphenoid in ventral view of A) *Archeria*, B) *Diadectes*, C) *Casea*, D) *Varanops*, E) *Ophiacodon*, F) *Edaphosaurus*, and G) *Dimetrodon*. Drawing of *Archeria* based on MCZ 8736; *Diadectes* based on MCZ 3277; *Casea* based on UC 698; *Varanops* based on UR 2423; *Ophiacodon* based on UC 1638 and MCZ 4820; *Edaphosaurus* based on MCZ 1762; and *Dimetrodon* based on MCZ 1697.

Abbreviations: bs s, basisphenoid shelf; bs w, basisphenoid wings; bst tub, basiptyergoid tubercula.

nearly 90 degrees to each other such as in *Dimetrodon* being a second character-state. In *Diadectes* (Fig. 7B), *Archeria* (Fig. 7A), and *Eocaptorhinus* (Heaton, 1979), the basiptyergoid processes are curved. Thus, for the character of the curvature of the articular surfaces, the character-states have the distribution shown in Figure 2B, with the presence of curved articular surfaces being the primitive character-state and the flat articular surfaces of *Dimetrodon*, *Sphenacodon*, and *Edaphosaurus* being a derived character-state.

The second character is the orientation of the basiptyergoid processes: the laterally oriented basiptyergoid processes such as is seen in *Aerosaurus* being one character-state, anteroventrally oriented processes such as is seen in *Dimetrodon* being a second character-state, and ventrally oriented basiptyergoid processes with anteroposteriorly oriented articular surfaces such as is seen in *Ophiacodon* being a third character-state. In all the outgroups, the basiptyergoid processes extend ventrolaterally from the side of the cultriform process as in *Dimetrodon*. Thus, for the character of the orientation of the basiptyergoid processes, the character-states have the distribution shown in Figure 2B, with the presence of ventrolaterally oriented basiptyergoid processes being the primitive character-state. The laterally orientated basiptyergoid process seen in *Casea* and *Aerosaurus* is one derived character-state, and the ventrally oriented basiptyergoid process with anteroposteriorly oriented articular surfaces of *Ophiacodon* is a second derived character-state.

Shelf Between Basisphenoid Wings

In *Dimetrodon* (Fig. 7G), *Sphenacodon*, and *Edaphosaurus*, the basisphenoid wings extend posteriolaterally from the base of the basiptyergoid tubercula with a smooth trough between them. In *Ophiacodon*, the arrangement of the basisphenoid wings is similar, but a shelf (bs.s., Fig. 7E) extends between the base of the wings, roofing over the anterior end of the trough. This is also the case in *Varanops* (Fig. 7D) and *Aerosaurus* (Langston and Reisz, 1981). In *Casea* (Fig. 7C), a basisphenoid shelf is present, although its posterior edge, rather than being straight, is V-shaped with the lateral ends of the V raised.

In *Limnoscelis* (Romer, 1946), a shelf is present roofing the anterior portion of the trough between the basisphenoid wings. In *Diadectes*, this shelf is hypertrophied and extends to the posterior ends

of the basisphenoid wings so that, in ventral view, the shelf appears to occupy the position of the wings (Fig. 7B). The anthracosaur *Archeria* is like *Limnoscelis* in having a shelf covering the anterior portion of the trough between the basisphenoid wings (Fig. 7A). *Paleothyris* is without such a shelf.

Thus, these character-states have the distribution shown in Figure 2F, with the presence of a shelf between the bases of the basisphenoid wings being the primitive character-state, and the absence of the shelf being a derived condition.

Stapes

The stapes of *Dimetrodon* (Fig. 8E) consists of a triangular plate oriented anteromedially with a posteromedially oriented footplate (fp., Fig. 8E) directed about 90 degrees from the medial edge of the triangular plate. The wide end of the triangle is the dorsal process (dp., Fig. 8E), and the narrow end is the quadrate process (qp., Fig. 8E). The dorsal process articulates in a socket on the ventral surface of the paroccipital process.

The stapes of *Edaphosaurus* (Fig. 8C) differs from that of *Dimetrodon* only in proportions, the dorsal process being relatively wider

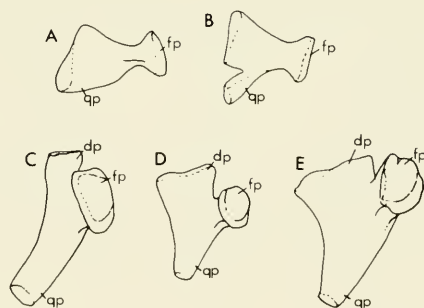


Figure 8. The left stapes in posterior view of A) *Casea*; B) *Varanops*; C) *Ophiacodon*; D) *Edaphosaurus*; E) *Dimetrodon*. Drawing of *Casea* based on UC 698; *Varanops* based on UR 2423; *Ophiacodon* based on MCZ 1366; *Edaphosaurus* based on MCZ 1762; and *Dimetrodon* based on MCZ 1347.

Abbreviations: dp, dorsal process; fp, footplate; qp, quadrate process.

and the quadrate process shorter. The dorsal process articulates in a socket on the paroccipital process as in *Dimetrodon*.

In *Ophiacodon* (Fig. 8C), the stapes is more rodlike than *Dimetrodon*. The dorsal process of the stapes is narrower, although it still articulates in a socket on the paroccipital process, and the footplate is oval, rather than circular in end view as in *Dimetrodon* and *Edaphosaurus*.

In *Casea* (Fig. 8A), the stapes consists of a footplate and a single triangular flange of bone extending laterally from this. One corner of the flange approaches the paroccipital process and presumably represents the base of the unossified dorsal process. The other corner is directed towards the stapedia pit of the quadrate. A distinct socket in the paroccipital process for the dorsal process of the stapes is not present.

The stapes of *Varanops* (Fig. 8B) differs from that of *Casea* in the presence of a V-shaped notch in its lateral edge. The edges of this notch are damaged, and therefore the notch may be artificial. In other regards, the stapes is directly comparable to that of *Casea*. As in *Casea*, no socket is present on the paroccipital process for the dorsal process of the stapes.

The stapes of *Aerosaurus* is not known, but the paroccipital process shows no articular surface for the dorsal process of the stapes (Langston and Reisz, 1981).

The stapes of *Paleothyris* (Carroll, 1969) appears most similar to the rodlike laterally directed stapes in captorhinids (Heaton, 1979), in which the dorsal process does not articulate in a socket on the paroccipital process. The stapes of *Diadectes*, as described by Olson (1966) is not readily comparable to that of any other tetrapod. A stapes is not known in *Limnoscelis* or anthracosaurs. In the early temnospondyle *Greererpeton*, the stapes is similar to that of *Varanops* and *Casea* in the presence of a triangular lateral process that does not have an ossified dorsal head articulating in a socket on the paroccipital process (Carroll, 1980). Since *Greererpeton* and pelycosaurs are both without an otic notch, probably primitively so (Lombard and Bolt, 1979; Carroll, 1980), the similarity of the stapes in these animals can be used as evidence that the stapes of *Casea* and *Varanops* is primitive in not having a socket on the paroccipital process that receives the dorsal process of the stapes.

Prearticular

In *Dimetrodon* (Fig. 9C), *Sphenacodon*, and *Edaphosaurus*, the prearticular underlies the pterygoideus process of the articular, a distinctive twisting of the bone being present as it passes under the process.

In *Ophiacodon* (Fig. 9A), the prearticular underlies the medial portion of the articular but does not show the twisting seen in *Dimetrodon*. This is also the case in *Varanops* (Fig. 10) and *Aerosaurus* (Langston and Reisz, 1981). The condition in *Casea* is unknown.

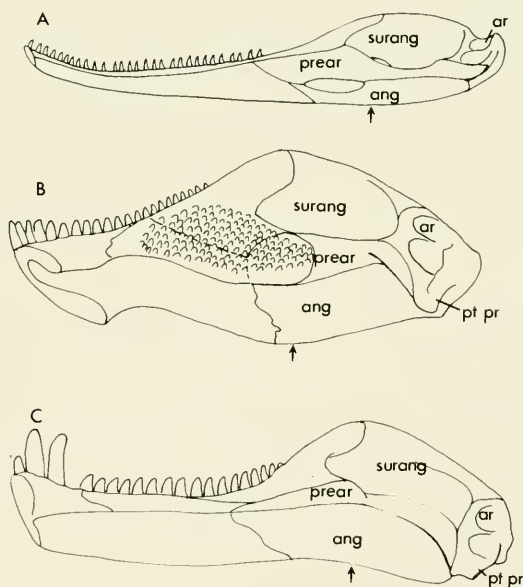


Figure 9. The right lower jaw in medial view of A) *Ophiacodon*; B) *Edaphosaurus*; C) *Dimetrodon*. From Romer and Price, 1940.

Abbreviations: ang, angular; ar, articular; prear, prearticular; pt pr, pterygoideus process; sur ang, surangular. Arrows indicate the position of sections shown in Figure 11.

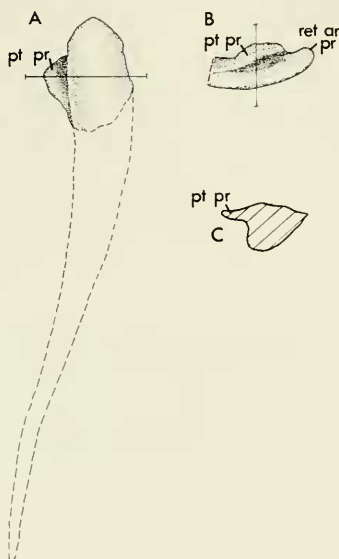


Figure 10. The lower jaw of *Varanops* in A) ventral view; B) medial view of articular region; and C) section through articular and pterygoideus process. Drawings based on MCZ 1926.

Abbreviations: pt pr, pterygoideus process; ret ar pr, retroarticular process.

Didaectes is without the twisting of the prearticular, as are captorhinids (Heaton, 1979), and anthracosaurs (Panchen, 1970). Thus, these character-states have the distribution shown in Figure 2B, with the absence of a twisted prearticular being the primitive character-state.

Angular

In *Dimetrodon* (Fig. 11E) and *Sphenacodon* the angular is a vertically oriented plate that supports the prearticular and surangular by its dorsal edge (Fig. 11E), and the articular by its medial surface. The posterior edge of the angular is notched, forming the reflected lamina of the angular.

The angular of *Edaphosaurus* (Fig. 11D) and *Ophiacodon* (Fig. 11C) is like that of *Dimetrodon* in being a vertically oriented plate. They differ in that they are without a posterior notch.

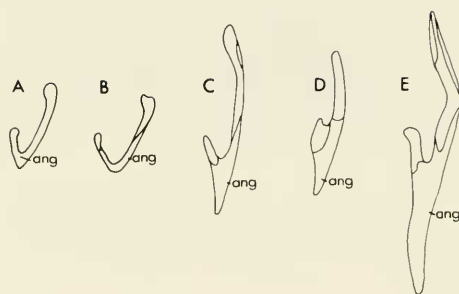


Figure 11. Sections through the postdentary bones of the lower jaw at the position just posterior to the dentary (marked by an arrow for the jaws shown in Figure 9). A) *Varanops*; B) *Casea*; C) *Ophiacodon*; D) *Edaphosaurus*; and E) *Dimetrodon*. Drawing of *Varanops* based on UR 2423; *Casea* based on UC 698; *Ophiacodon*, *Dimetrodon* and *Edaphosaurus* from Romer and Price, 1940.

Abbreviation: ang, angular.

In *Casea* (Fig. 11A), *Varanops* (Fig. 11B), and *Aerosaurus* (Langston and Reisz, 1981), the angular is a troughlike bone. In *Varanops*, a keel is present on its ventral edge, but in no position along the angular does the bone form an extended vertical plate.

The angular in *Limnoscelis* and *Diadectes* is like that of *Casea* and *Varanops* in being troughlike. In *Paleothyris*, a keel is present in the region of the angular, but the bone does not form an extended vertical plate. Thus, these character-states have the distribution shown in Figure 2B, with the absence of an extended vertical plate being the primitive character-state.

Pterygoideus Process of Articular

In *Dimetrodon* (Fig. 9C), *Sphenacodon*, and *Edaphosaurus* (Fig. 9C), a pterygoideus process is present as a distinct process on the articular. In primitive species of *Dimetrodon*, and in *Sphenacodon* and *Edaphosaurus*, this is located medial to the glenoid.

In *Ophiacodon* (Fig. 9A) a distinct pterygoideus process is not present on the articular. A flange on the prearticular just anterior to the articular may be functionally equivalent to the pterygoideus process of *Dimetrodon*.

In *Varanops* (Fig. 10) and *Aerosaurus* (Langston and Reisz, 1981), a pterygoideus process is not present on the articular,

although a well-developed flange on the prearticular just anterior to the articular is present. The condition in *Casea* is unknown.

In *Diadectes*, the articular does not have a distinct pterygoideus process. The articular extends medially from the inner surface of the jaw (Romer, 1956; Fig. 107C), but the medially projecting portion is located beneath the medial condyle of the glenoid and is not a distinct process. No flange is present on the prearticular anterior to the articular. This is also the case in anthracosaurs (Panchen, 1970). The internal surface of the articular is not known in *Paleothyris*. In captorhinids, a pterygoideus process is absent or poorly developed, although a medial flange formed by the prearticular just anterior to the articular is present (Heaton, 1979). Thus, these character-states have the distribution shown in Figure 2D, with the absence of a pterygoideus process being primitive for tetrapods, the presence of a flange on the prearticular just anterior to the articular being primitive for reptiles, and the presence of a pterygoideus process formed by the articular being a derived feature within pelycosaurs.

Neural Arch

In *Dimetrodon* (Fig. 12F) and *Sphenacodon*, the neural arch has a pit in its lateral surface above the level of the transverse process. In *Edaphosaurus boanerges* (Fig. 12E), the neural arch is without pits, although in an undescribed species of *Edaphosaurus* from near Garnett, Kansas, *Sphenacodon*-like pits are present along the length of the column (Reisz *et al.*, 1982). *Varanops* (Fig. 12C) and *Aerosaurus* (Langston and Reisz, 1981) are like *Dimetrodon* in having a pit in the lateral surface of the neural arch. *Ophiacodon* (Fig. 12D) and *Casea* (Fig. 12B) are without a pit in the lateral surface of the neural arch.

The neural arches of *Limnoscelis*, *Diadectes*, anthracosaurs, and *Paleothyris* are without pits. Thus, these character-states have the distribution shown in Figure 2B, with the absence of pits in the neural arch being the primitive character-state.

Transverse Processes

In *Dimetrodon* (Fig. 12F) and *Sphenacodon*, the longest transverse processes are in the area of the posterior cervicals and anterior dorsals. They extend laterally a distance about equal to the width of the centrum.

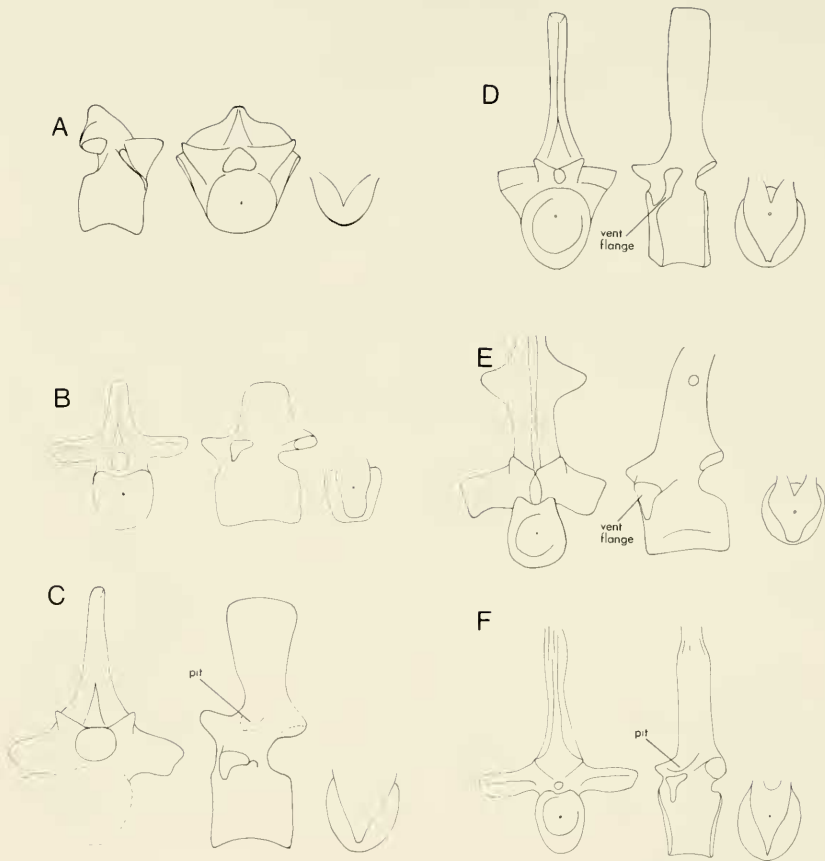


Figure 12. Anterior dorsal vertebrae in lateral and anterior view, and a cross section of an anterior dorsal centrum of A) *Labidosaurus*; B) *Casea*; C) *Varanops*; D) *Ophiacodon*; E) *Edaphosaurus*; and F) *Dimetrodon*. Drawing of *Labidosaurus* based on MCZ 8724; *Casea* based on P 12841; *Varanops* based on MCZ 1926; *Ophiacodon* based on MCA 5912; *Edaphosaurus* based on MCZ 1359; and *Dimetrodon* based on MCZ 5216.

Abbreviations: pit, pit in the lateral surface of the neural arch; vent flange, ventral flange supporting the transverse process.

In *Edaphosaurus*, the longest transverse processes are shorter than the width of the centrum and the transverse processes are braced by a vertical flange of bone ventrally.

Ophiacodon (Fig. 12D) has short transverse processes directed more ventrally than in *Edaphosaurus* and *Dimetrodon*. The ventral flange forms a complete web of bone connecting the transverse processes to the anterior edge of the centrum.

Varanops (Fig. 12C), *Aerosaurus* (Langston and Reisz, 1981), and *Casea* (Fig. 12B) have long laterally directed transverse processes. *Limnoscelis*, *Diadectes*, anthracosaurs, and *Paleothyris* all have short transverse processes, although only in captorhinids (Fig. 12A) are these supported by a web of bone that extends to the anterior edge of the centrum. Thus, for the character of the transverse processes, the character-states have the distribution shown in Figure 2D, with the presence of short transverse processes connected to the anterior edge of the centrum by a web of bone being the primitive character-state for reptiles, and the long transverse processes being a derived character-state present within pelycosaurs.

Centrum

In *Dimetrodon* (Fig. 12F) and *Sphenacodon*, the vertebrae in the cervical and anterior to mid-dorsal regions of the vertebral column have well-developed keels.

In *Edaphosaurus* (Fig. 12E), keels are present only on the cervical vertebrae. The dorsal vertebrae have broadly rounded ventral surfaces.

In *Ophiacodon* (Fig. 12D), the cervical vertebrae are keeled. The mid-dorsal vertebrae are wedge-shaped in cross section but have a pair of ridges ventrally, rather than a single keel. The posterior dorsal and lumbar vertebrae are circular in end view.

In *Varanops* (Fig. 12C), the cervical and mid-dorsal vertebrae are keeled.

In *Casea* the most anterior cervical vertebrae are unknown. All the more posterior vertebrae are without keels (Fig. 12B). In cross section, the centra have flatter ventral surfaces than in *Edaphosaurus*.

The centra of *Diadectes* and *Limnoscelis* are not specifically similar to any pelycosaur. In cross section, they are generally wedge-shaped, but are without a distinct keel. The vertebrae of *Protero-*

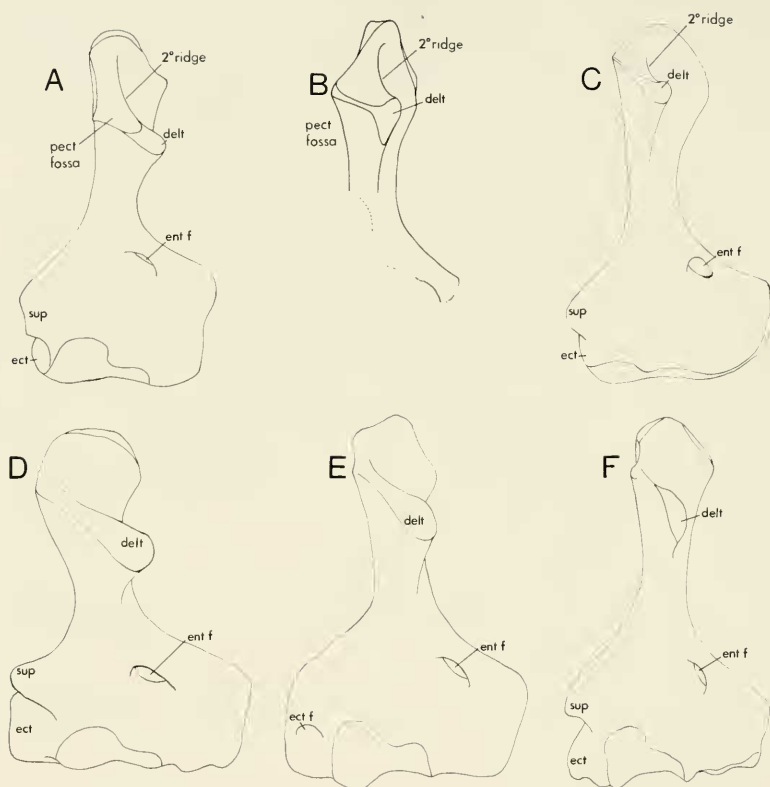


Figure 13. The humerus in distal ventral view of A) *Casea*; B) *Arosaurus*; C) *Varanops*; D) *Ophiacodon*; E) *Edaphosaurus*; and F) *Dimetrodon*. Drawing of *Casea* from Williston (1911), drawing of *Arosaurus* based on UC 464; *Varanops* based on UR 695; *Ophiacodon* based on MCZ 1486; *Edaphosaurus* based on MCZ 3417; *Dimetrodon* based on MCZ 1304.

Abbreviations: delt, deltopectoral crest; ect, ectepicondyle; ect f, ectepicondylar foramen; ent f, entepicondylar foramen; pect fossa, pectoralis fossa; sup, supinator process; 2° ridge, secondary pectoralis ridge.

gyrinus an anthracosaur with a protoreptilian vertebral pattern (Holmes and Carroll, 1977), are without keels. This is also the case in captorhinids (Fig. 12A). Thus, the absence of a distinct keel can be considered a primitive feature.

Deltopectoral Crest

In *Sphenacodon* and *Dimetrodon* (Fig. 13F), the deltopectoral crest has a bulbous distal end and a sharp knife-edge base. In *Ophiacodon* and *Edaphosaurus*, the distal end of the deltopectoral crest is bulbous, but the proximal end is a broad ridge (Fig. 13 D-E).

In *Varanops* (Fig. 13C), *Aerosaurus* (Fig. 13B), and *Casea* (Fig. 13A), a secondary ridge is present extending from the distal end of the deltopectoral crest to a more medial position on the proximal end of the humerus. In *Casea* and *Aerosaurus*, this is a sharp crest that results in the presence of a distinct fossa at the base of the deltopectoral crest. In *Varanops* this is a low, rounded ridge.

In captorhinids (Holmes, 1977), the crest is absent. The tuberosity is located on the lateral edge of the proximal end of the humerus. In *Diadectes*, the deltopectoral crest is like that of *Ophiacodon*, although it forms a more obtuse angle with the proximal end of the humerus. Thus, these character-states have the distribution shown in Figure 2E, with the presence of a deltopectoral crest formed by a single broad ridge extending from the tuberosity to the proximal end of the bone being a primitive reptilian condition, and the presence of a secondary ridge extending from the deltopectoral tuberosity to the proximal end of the bone being a derived condition.

Results

The distribution of the character-states for which polarity can be interpreted, and the cladogram that requires the fewest number of reverseals or convergent evolutionary events to explain this distribution, is shown in Figure 14.

CHARACTER ANALYSIS: II. FEATURES FOR WHICH POLARITY CANNOT BE INTERPRETED

As argued in the materials and methods section, characters for which polarity of the character-states cannot be interpreted are of use in providing a test of the cladogram presented on the basis of other characters. Three such characters are considered here.

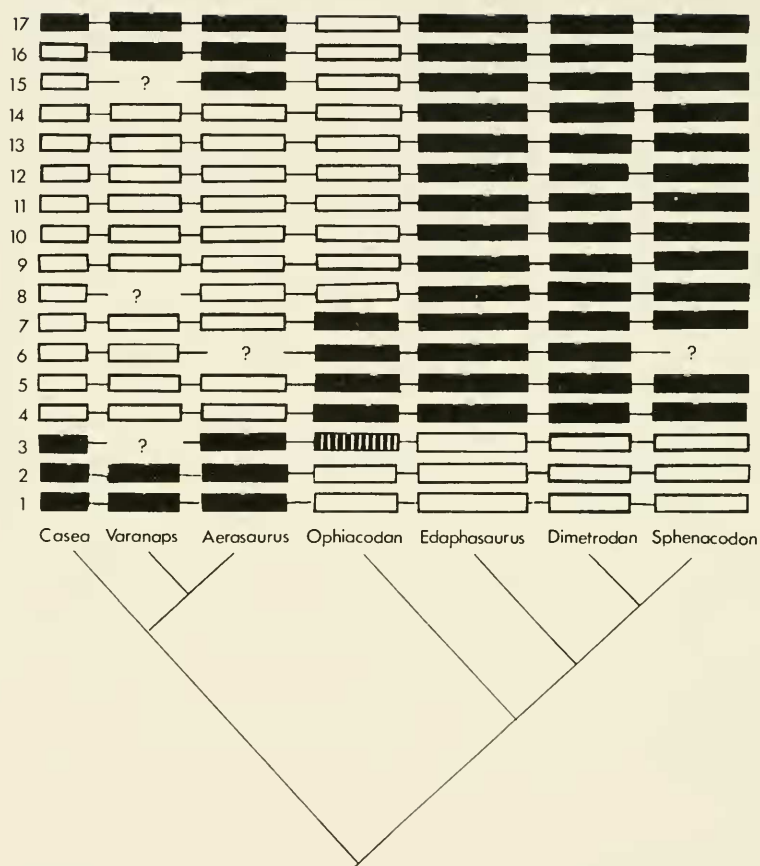


Figure 14. Hypothesis of relationships of selected genera of pelycosaurs based on the characters described in the text for which polarity can be interpreted. □ indicate primitive character-states, ■ and ▨ indicate derived character-states. For description of characters and character-states see Table 2.

Table 2. The characters that form the basis for the cladogram shown in Figure 14. The numbers refer to the characters shown in Figure 14.

1) humerus, deltopectoral crest:

primitive character-state: the presence of a single ridge leading from the distal end of the deltopectoral crest to the proximal end of the humerus;

derived character-state: the presence of a secondary ridge leading from the distal end of the deltopectoral crest to a more medial position on the proximal end of the humerus with a fossa at the base of the crest.

2) maxilla:

primitive character-state: no contact between the maxilla and the quadratojugal;

derived character-state: the maxilla contacts the quadratojugal with the bones raised to form a ridge along the contact of the maxilla and jugal.

3) basiptyergoid process:

primitive character-state: basiptyergoid process directed anteroventrally;

derived character-state #1 (indicated by ■ in Figure 14): basiptyergoid process directed laterally and are mediolaterally elongate;

derived character-state #2 (indicated by ▣ in Figure 14): basiptyergoid processes directed ventrally and articular surface oriented anteroposteriorly.

4) cheek margin:

primitive character-state: cheek margin convex;

derived character-state: cheek margin concave.

5) premaxilla:

primitive character-state: anterior margin of the premaxilla extends anteriorly from the anterior termination of the tooth row;

derived character-state: anterior margin of the premaxilla slopes posteriorly from the anterior termination of the tooth row.

6) stapes:

primitive character-state: dorsal process of stapes not articulating in socket on the paroccipital process;

derived character-state: dorsal process of stapes articulating in a socket on the paroccipital process.

7) angular:

primitive character-state: angular without an extended ventral plate in the region anterior to the articular;

derived character-state: angular with an extended ventral plate in the region of the articular.

8) basiptyergoid articular surfaces:

primitive character-state: articular surfaces curved;

derived character-state: articular surfaces differentiated into two flat areas at right angles to each other.

9) shelf between basisphenoid wings:

primitive character-state: shelf between basisphenoid wings present;

derived character-state: no shelf between basisphenoid wings.

Table 2. Continued

-
- 10) frontal:
primitive character-state: frontal without a lateral lappet;
derived character-state: frontal with a lateral lappet.
- 11) quadratojugal:
primitive character-state: quadratojugal extends anteriorly forming ventral margin of skull along posterior half of cheek;
derived character-state: quadratojugal restricted to ventro-lateral corner of skull.
- 12) prearticular:
primitive character-state: prearticular not twisted;
derived character-state: prearticular twisted.
- 13) pterygoideus process:
primitive character-state: pterygoideus process not formed by articular alone;
derived character-state: pterygoideus process formed entirely by articular.
- 14) quadrate ramus of pterygoid:
primitive character-state: quadrate ramus of pterygoid with a medially directed tympanic flange along its ventral edge;
derived character-state: quadrate ramus of pterygoid with rounded ventral edge.
- 15) supraoccipital:
primitive character-state: supraoccipital without a lateral process, dorsal border of posttemporal fenestra formed by tabular;
derived character-state: supraoccipital with a lateral process that forms the dorsal border of the posttemporal fenestra.
- 16) neural arch:
primitive character-state: neural arch without pits;
derived character-state: neural arch with pits on its lateral surface at the level of the zygapophyses.
- 17) transverse processes:
primitive character-state: transverse processes supported by a web of bone extending to the anterior edge of the centrum;
derived character-state: transverse processes extend laterally, ventral flange not extending to the anterior edge of the centrum.
-

Postparietal

In *Dimetrodon*, *Sphenacodon* (Fig. 6D), and *Edaphosaurus* (Fig. 6C), the postparietal is a single median element that broadly overlies the supraoccipital.

The *Ophiacodon*, a postparietal was not observed, but the supraoccipital shows that the postparietal did not greatly overlap that bone.

In *Casea* (Fig. 6A), the postparietal is a paired element.

The postparietal of *Varanops* and *Aerosaurus* is unknown.

Limnoscelis is like *Dimetrodon* and *Edaphosaurus* in having a single postparietal (Romer, 1946). In anthracosaurs, as in primitive tetrapods generally, the postparietal is a paired element (Panchen, 1970).

Two explanations for this distribution of character-states are equally possible: that *Limnoscelis* is apomorphic in having a single postparietal and a paired postparietal is primitive for reptiles, or that a single postparietal is primitive for reptiles and *Casea* is derived in having a paired postparietal. In view of this, the presence of single or paired postparietals must be considered character-states for which polarity cannot be determined.

Paroccipital processes

The paroccipital processes in *Dimetrodon* and *Sphenacodon* are rodlike structures sloping ventrally and posteriorly. In cross section, they are triangular with their height less than twice their width. In *Edaphosaurus*, the processes are like those in *Dimetrodon*, but they are shorter and extend more directly laterally (Fig. 6C). In *Ophiacodon*, the process is short and laterally directed (Fig. 6B). It is rodlike, although its distal end is unossified so that, as preserved, it does not reach the cheek. In *Varanops* (Fig. 4B) and *Aerosaurus* (Langston and Reisz, 1981), the paroccipital process is platelike: in lateral view its height is more than three times its width. In *Casea*, the platelike nature of the paroccipital process is exaggerated (Fig. 6A).

Thus, two distinct character-states can be recognized: one present in *Varanops* and *Casea* in which the paroccipital process is platelike, and one seen in *Ophiacodon*, *Edaphosaurus*, *Dimetrodon*, and *Sphenacodon* in which the paroccipital process is rodlike. The paroccipital process of *Limnoscelis*, as described by Romer (1946), is not directly comparable to either pelycosaur condition. The paroccipital process of *Paleothyris* is unossified (Carroll, 1969). Thus, there is no basis for interpreting the polarity of these character-states.

Supinator Process

In *Dimetrodon* and *Sphenacodon*, the supinator process is elongate proximodistally, and its distal end curves distally (Fig. 13F).

In *Edaphosaurus* (Fig. 13E), an ectepicondylar foramen is present. Romer and Price (1940) interpreted this as a result of the development of a bony connection between the ectepicondyle and the distal end of the supinator process. Without this connection, the supinator process would have the morphology of that of *Dimetrodon*.

In *Ophiacodon* (Fig. 13D), the supinator process is a narrow triangular process that projects laterally.

Casea (Fig. 13A) and *Varanops* (Fig. 13C) are like *Dimetrodon* in the development of their supinator process. The morphology of the process in an adult humerus of *Aerosaurus* is not known.

The structure of the supinator process is variable in early tetrapods. In anthracosaurs, this is represented by a crest running the full length of the humerus (Panchen, 1970). In *Limnoscelis* and *Diadectes*, it is a narrow laterally directed process located distal to the radial condyle (Romer, 1956). In its shape, it is like that of *Ophiacodon*, but in *Ophiacodon*, as in other pelycosaurs and in contrast to *Diadectes* and *Limnoscelis*, the supinator process is located distally and is separated from the radial condyle by a distinct groove. The supinator process of *Paleothyris* is located near the distal end of the humerus and is separated from the radial condyle by a groove (Carroll, 1969). Its shape does not compare directly with either pelycosaur condition. This distribution of character-states does not allow polarity of the character in pelycosaurs to be interpreted.

Results

The characters for which polarity cannot be interpreted can be separated into two groups: those whose distribution does not require hypothesizing the occurrence of parallel evolution, and those whose distribution requires a more complicated hypothesis of evolution of the character. In the first group are the structure of the paroccipital process and the presence of paired postparietals. The structure of the paroccipital process is in accordance with the separation of *Ophiacodon*, *Edaphosaurus*, *Dimetrodon*, and *Sphenacodon* from *Aerosaurus*, *Varanops*, and *Casea*, and thus is in agreement with the separation of pelycosaurs into these two groups.

In the second group is the structure of the supinator process. If the supinator process of *Ophiacodon* is autapomorphic, these character-states are consistent with the cladogram; if primitive, then

the proximodistally elongate supinator process must have evolved independently in the clade including *Casea* and *Varanops* and the clade including *Edaphosaurus*, *Dimetrodon*, and *Sphenacodon*. Thus, this character is not necessarily in conflict with the cladogram, but requires a more restrictive hypothesis of polarities to account for the distribution of the character-states.

DISCUSSION

These results differ from those of Reisz (1980) in three features: 1) *Edaphosaurus* and *Dimetrodon* are interpreted as members of a clade more derived than *Ophiacodon*; 2) *Varanops* and *Aerosaurus* are interpreted as being more primitive than the clade including *Ophiacodon*, *Edaphosaurus*, *Dimetrodon*, and *Sphenacodon*; and 3) *Casea*, *Varanops*, and *Aerosaurus* are interpreted as being members of a single clade distinct from the clade including *Ophiacodon*, *Edaphosaurus*, and *Dimetrodon*.

The more primitive position of *Ophiacodon* relative to *Edaphosaurus* and *Dimetrodon* is the same as that in the phylogeny proposed by Romer and Price (1940). The alternate interpretation of relationships of these genera proposed by Reisz (1980) was based primarily on cranial features, including the structure of the frontal, supratemporal, and the proportions of the skull. The structure of the frontal of *Edaphosaurus* was incorrectly interpreted by Romer and Price (1940). As discussed above, the frontal of *Edaphosaurus* is directly comparable to that of *Dimetrodon*, and the frontals in these animals share features that can be interpreted as being derived with respect to *Ophiacodon*. Thus, the frontal supports a relationship between *Edaphosaurus* and *Dimetrodon*, rather than between *Ophiacodon* and *Dimetrodon*. The structure of the supratemporal is poorly known in most genera. The element that Romer and Price identified as the supratemporal in *Casea* is better interpreted as the proximal end of the squamosal. This is also the case in *Edaphosaurus*. Thus, this character cannot be used at present in interpreting pelycosaur interrelationships. The proportions of the skull of *Edaphosaurus* are not known with sufficient certainty to be used in interpreting relationships.

The position of *Varanops* and *Aerosaurus* is the most striking difference from both the cladogram of Reisz (1980) and the phylogeny of Romer and Price (1940). This difference is based on the

interpretation that *Ophiacodon* and *Dimetrodon* share derived cranial features not present in *Varanops* and *Aerosaurus*, and that *Casea*, *Varanops*, and *Aerosaurus* share derived cranial features not present in *Ophiacodon*. Necessarily, we interpret the derived vertebral features shared in *Dimetrodon* and *Varanops*, the features that Romer and Price used to unite these genera, as convergent.

The suggestion that *Casea*, *Varanops*, and *Aerosaurus* are members of a single clade is the least well supported of the relationships proposed above. This reflects the problems inherent in determining relationships of primitive members of clades. Greater certainty about the primitive character-state of various features in pelycosaurs will come from a better understanding of the interrelationships of early reptiles and the use of an out-group that is more closely related to pelycosaurs than are diadectomorphs in the analysis of polarities. This will allow better separation of characters that are primitive for pelycosaurs from those that are derived for the clade including *Casea* and *Varanops*.

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LITERATURE CITED

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